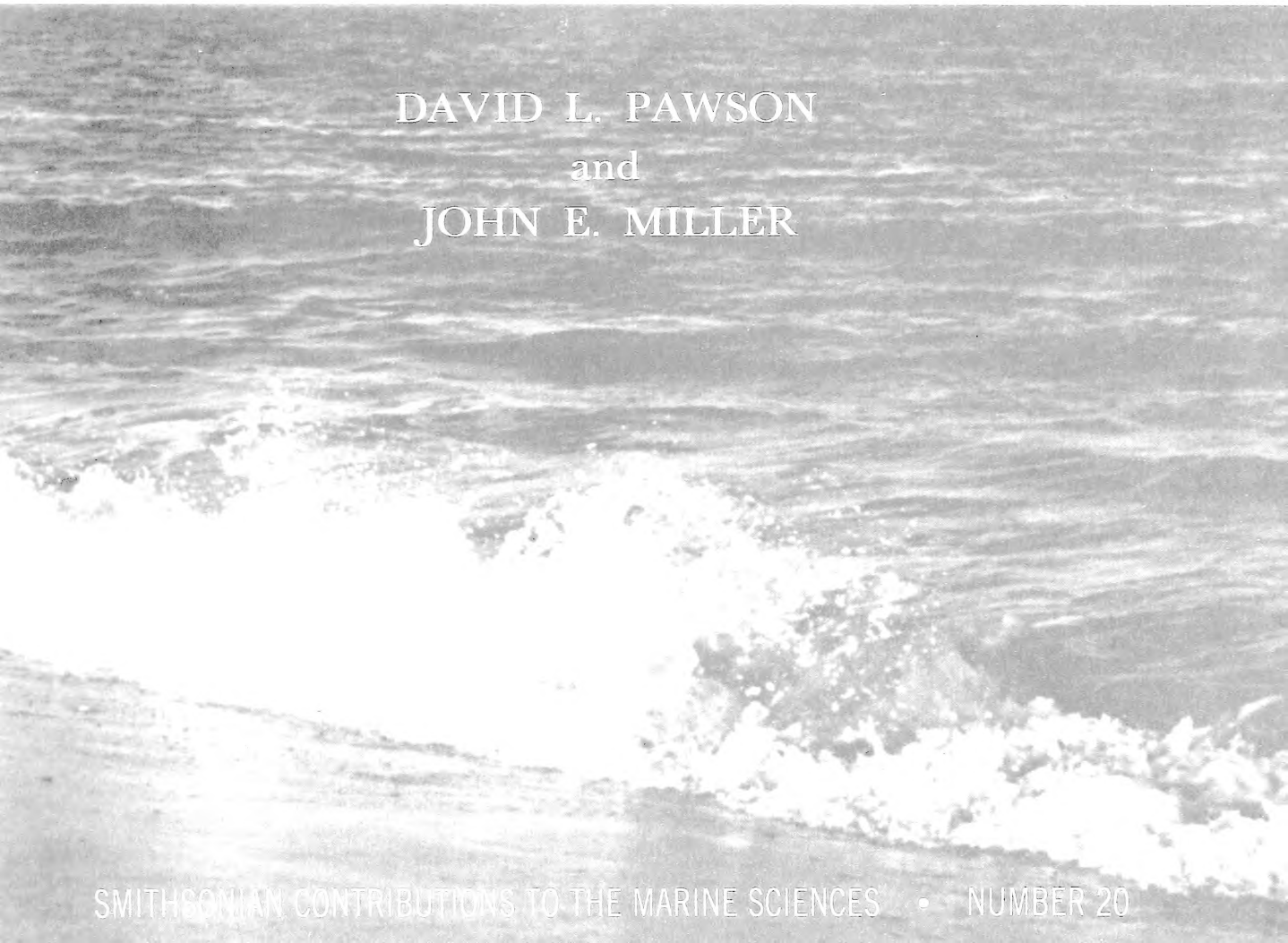
Systematics and Ecology of the Sea-Urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans



DAVID L. PAWSON
and
JOHN E. MILLER

SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 20

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 20

Systematics and Ecology of the Sea-Urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans

David L. Pawson
and John E. Miller

SMITHSONIAN INSTITUTION PRESS
City of Washington
1983

ABSTRACT

Pawson, David L., and John E. Miller. Systematics and Ecology of the Sea-Urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans. *Smithsonian Contributions to the Marine Sciences*, number 20, 15 pages, 5 figures, 5 tables, 1983.—Surveys by the *Johnson-Sea-Link* submersibles have revealed the presence of large populations of black *Centrostephanus*, superficially resembling *Diadema antillarum* Philippi, along the shelf edge prominences off the east coast of Florida in depths of 48–80 meters. Typical habitats are aggregations of dead coral rubble, with seasonal growths of leafy red algae. Some aspects of the biology of these echinoids are described.

We affirm that only a single species of the genus, *Centrostephanus longispinus* (Philippi), occurs in the Atlantic Ocean. As Fell (1975) and Serafy (1979) have shown, western Atlantic populations can be referred to the subspecies *Centrostephanus longispinus rubicingulus* H.L. Clark, which usually differs from the typical subspecies in possessing uniformly black spines rather than banded purple and yellowish white spines when fully grown. *C. besnardi* Bernasconi from Isla Trindade, Brazil, is herein synonymized with *C. longispinus rubicingulus*. *C. coronatus* (Verrill) from California and the Galapagos Islands differs little from *C. longispinus* and the two species may yet prove to be subjective synonyms. There is some evidence to suggest that Gulf of California populations of *C. coronatus* differs from California populations at the subspecies level.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: Seascape along the Atlantic coast of eastern North America.

Library of Congress Cataloging in Publication Data
Pawson, David L. (David Leo), 1938–
Sea urchin genus Centrostephanus (Echinodermata: Echinoidea)
(Smithsonian contributions to the marine sciences ; no. 20)
Bibliography: p.
Supt. of Docs. no.: ST 1.41:20
1. Centrostephanus. 2. Echinodermata—Atlantic Ocean. 3. Echinodermata—Pacific Ocean. I. Miller, John E. II. Title. III. Series.
QL384.E2P38 1983 593.9'5 83-600054

Contents

Systematics and Ecology of the Sea-Urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans

David L. Pawson
and John E. Miller

Introduction

During investigations of the structure and faunas of shelf-edge prominences along the east coast of Florida (see Avent et al., 1977; Reed, 1980), a long-spined black sea urchin was found to be a notable and numerous inhabitant of coral rubble zones. Using Harbor Branch Foundation, Inc. submersibles *Johnson-Sea-Link* I and II, we have been able to collect specimens of this urchin, to observe them in their natural habitat, and maintain them alive in aquaria. Closer examination revealed that the urchin is a species of *Centrostephanus*, a widespread Atlantic and Indo-Pacific diadematid genus.

In this paper we describe this newly found material of *Centrostephanus* and discuss some aspects of its biology and systematic position. In addition, we compare our Florida specimens with *C. longispinus* from the eastern Atlantic and *C. coronatus* from the eastern Pacific.

ACKNOWLEDGMENTS.—Determinations of algal species were kindly made by S.M. Blair, Harbor Branch Foundation. We thank F.M. Bayer, Smithsonian Institution, for his helpful insight with several nomenclatural problems. Loan of museum specimens was made possible by Robert M. Woollacott, Museum of Comparative Zoology, Harvard, and Alberto Larrain, Allan Hancock Foundation, University of Southern California. We are indebted to the crews of *Johnson-Sea-Link* submersibles and R/V *Johnson* for their professional skills during submersible operations. We are grateful to G. Hendler and R.L. Turner for critically reviewing the manuscript. Funding for this study was granted by the Smithsonian Institution and Harbor Branch Foundation, Inc. This paper represents Contribution No. 118 from the Smithsonian Marine Station at Link Port and Contribution No. 336 from Harbor Branch Foundation, Inc.

David L. Pawson, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. John E. Miller, Harbor Branch Foundation, Inc., R.R. 1, Box 196, Fort Pierce, Florida, 33450.

Centrostephanus Peters, 1855

DIAGNOSIS.—Like *Diadema*, but with buccal plates carrying spines and pedicellariae. Globiferous pedicellariae present.

TYPE-SPECIES.—*Centrostephanus longispinus* (Philippi).

COMPOSITION OF THE GENUS.—*Centrostephanus*

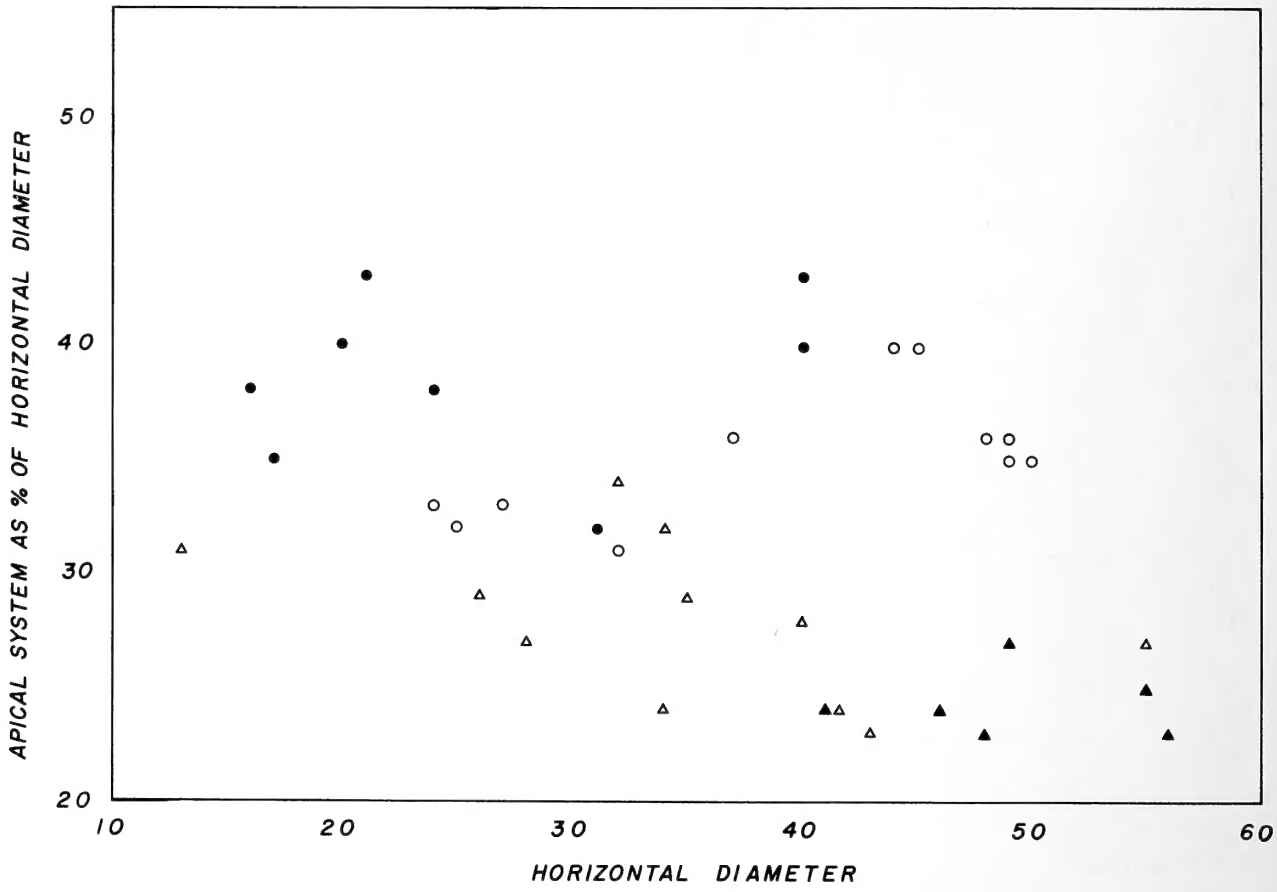


FIGURE 1.—Relationship of apical system to horizontal diameter (in mm) in species of *Centrostephanus* (closed circles = *C. longispinus longispinus* (Philippi) from eastern Atlantic; open circles = *C. longispinus rubicingulus* H.L. Clark from east coast of Florida; closed triangles = *C. coronatus* (Verrill) from lower California coast; open triangles = *C. coronatus* from Gulf of California).

currently comprises ten nominal species, widely distributed in the Atlantic and Indo-Pacific. In his monograph of the Echinoidea, Mortensen (1940) described eight species of *Centrostephanus*. Later, Bernasconi (1955a,b) described *C. besnardi* from Isla Trindade, Brazil, and Fell (1975) described *C. sylviae* from San Felix and Juan Fernandez Islands, off Chile. Mortensen (1940) noted that *C. longispinus* and *C. rubicingulus* were apparently closely related; he believed that *C. rubicingulus* could be distinguished from *C. longispinus* by the presence in the former species of more numerous and larger secondary interambulacral tubercles. Fell (1975) briefly reviewed the genus and found that differences in size and number of secondary interambulacral tubercles were not reliable systematic characters. Fell (1975) suggested that *C. rubicingulus* should be reduced to a subspecies of *C. longispinus*, and he noted that the three nominal Atlantic Ocean species, *C. longispinus*, *C. rubicingulus*, and *C. besnardi*, along with juvenile *C. coronatus* from the eastern Pacific, "cannot be distinguished morphologically using adult characters. Identifications must be done by locality" (Fell, 1975:181). Serafy (1979) followed Fell's suggestion, and reduced *C. rubicingulus* to a subspecies of *C. longispinus* (Phillippi).

CLAVIFORM SPINES IN *Centrostephanus*.—Several authors, including Hamann (1887), Mortensen (1940), and Fell (1975) have called attention to

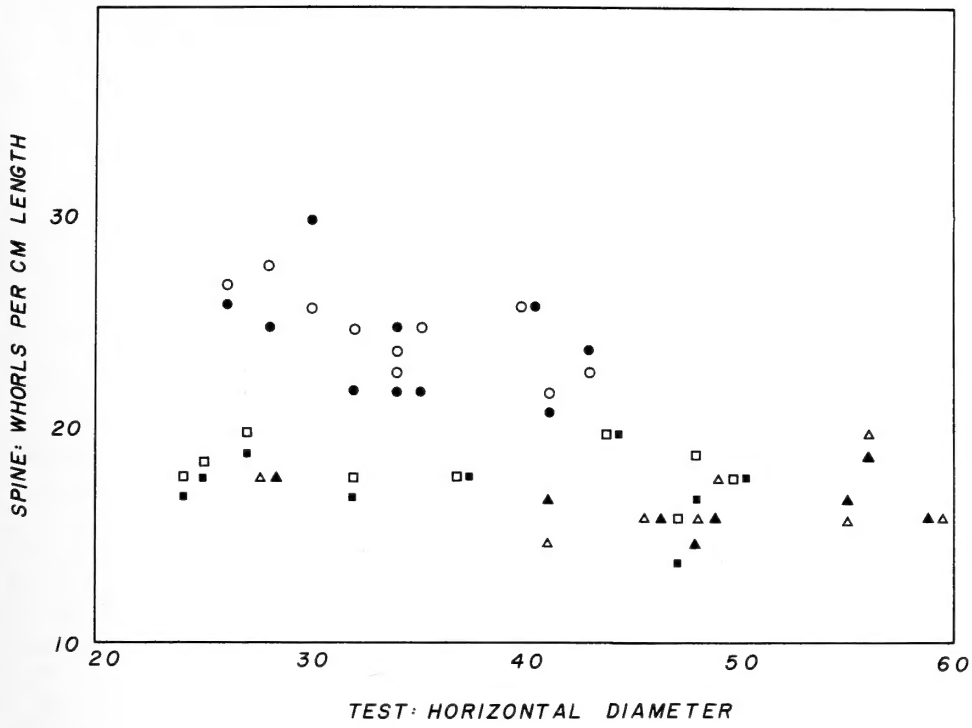


FIGURE 2.—Relationship of whorls of spinelets of spines (verticillations) to horizontal diameter of test in species of *Centrostephanus* (circles = *C. coronatus* from Gulf of California; triangles = *C. coronatus* from lower California coast; squares = *C. longispinus rubicingulus* from east coast of Florida; open symbols = ambulacral spines; closed symbols = adambulacral spines).

the presence of peculiar club-shaped spines on the adapical plates in some species of *Centrostephanus*. These highly motile spines, tipped with an intense pink or purple pigment, are found in only four of the ten nominal species: *C. longispinus*, *C. rubicingulus*, *C. besnardi*, and *C. coronatus*. These closely related "species" form a natural (Tethyan?) group occurring in the eastern Atlantic, the western Atlantic, and in the eastern Pacific. Fell (1975) noted that *C. asteriscus* Agassiz and Clark, 1907, from Hawaii and the Kei Islands, has some features in common with the species mentioned above but differs in lacking claviform spines. Fell (1975) referred the species that lack claviform spines, *C. rodgersii* (Agassiz, 1863), *C. tenuispinus* Clark, 1914, and *C. sylviae* Fell, 1975, to a single "superspecies." If the genus *Centrostephanus* were to be split into two genera or subgenera based upon the presence or absence of claviform spines, the genus name *Trichodiadema* Agassiz, 1863, type-species *rodgersii* Agassiz, is available for species that lack these spines.

CHANGES PROPOSED FOR THE GENUS *Centrostephanus*.—Results from our studies of live material and existing museum collections lead us to agree with the suggestions of Fell (1975). We accept Serafy's reassignment of *Centrostephanus rubicingulus* to a subspecies of *C. longispinus*, although the diagnoses of the subspecies require some modification. Further, we refer *C. besnardi* Bernasconi to synonymy with *C. longispinus rubicingulus* H.L. Clark, thereby restricting *Centrostephanus* to eight nominal species.

Centrostephanus longispinus (Philippi)

DIAGNOSIS.—Claviform spines present adapically. Apical system usually 30%–40% of test diameter. Spines usually with well-developed tra-

beculae between wedges. Eastern and western Atlantic Ocean.

REMARKS.—Two subspecies of *C. longispinus* may now be recognized.

Key to Subspecies of *C. longispinus*

Specimens of all sizes with banded spines, with purple bands on yellowish white or light green ground color; from the Mediterranean and eastern Atlantic ..... ***Centrostephanus longispinus longispinus*** (Philippi)

Small specimens (h.d. <25 mm) with banded spines, reddish brown on whitish ground color; larger specimens (h.d. >25 mm) with uniformly blackish spines or with banded spines, the bands brown on lighter brown ground color; from the western Atlantic .....
..... ***Centrostephanus longispinus rubicingulus*** H.L. Clark

Centrostephanus longispinus longispinus (Philippi)

FIGURE 1; TABLE 1

Diadema longispina Philippi, 1845:354.

Centrostephanus longispinus.—Mortensen, 1940:300, pl. 24: figs. 1–11; pl. 25: figs. 11, 12; pl. 75: figs. 5–24 [complete synonymy up to 1938]; 1951:296.—Tortonese, 1953:214; 1965:311, figs. 143–145; 1976:238.—Chapman, 1955: 399.—Cherbonnier, 1956:17; 1959:44, pl. 4: figs. B-L; pl. 5: figs. A, B; 1963:186.—Millott, 1957, fig. 4.—Repelin, 1962:4, pl. 1: fig. 6; pl. 2: figs. 7, 8.—Chesher, 1966:215.—Märkel, 1970:190, figs. 1, 2, 4, 5, 14a.

?Centrostephanus longispinus.—Alvardo and Alvarez, 1964: 278.

MATERIAL EXAMINED.—Universitetets Zoologiske Museum, Copenhagen, *Atlantide* Expedition, Sta. 61, 106, 116, Gulf of Guinea, 53–95 meters, seven specimens. Museum of Comparative Zoology, Harvard University, Cat. No. 689, 4573, Northeastern Atlantic, two specimens.

DIAGNOSIS.—Spines banded purple and yellowish white. Mediterranean and eastern Atlantic.

TYPE-LOCALITY.—Palermo, Sicily.

DESCRIPTION.—Specimens examined were typical of the subspecies as described by Mortensen (1940) and others. Information on numbers of test plates, diameter of apical system and peristome, and on structure of spines, is presented in Table 1.

DISTRIBUTION.—Western Mediterranean; eastern Atlantic, from Morocco to Gabon; Cape Verde Islands and the Azores (Mortensen, 1940, 1951; Chesher, 1966). Depth range 42–208 meters.

REMARKS.—This subspecies has been thoroughly described by Koehler (1895) and Mortensen (1904, 1940), and requires no further comment here. Unlike *C. longispinus rubicingulus* (see below), apparently no specimens with spines of a solid dark color have been found; in even the largest specimens the spines are banded.

Centrostephanus longispinus rubicingulus H.L. Clark

FIGURES 1–5; TABLES 2, 3

Centrostephanus rubicingulus H.L. Clark, 1921:108, pl. 1: figs. 1, 2.

Centrostephanus rubricingulus H.L. Clark, 1925:52.—Mortensen, 1940:308, pl. 36: figs. 3–6, 11, 12, pl. 76: figs. 10–12, 14–18, 22.—A.H. Clark, 1954:374.—Lewis, 1961:53.—Fell, 1975:180.

Centrostephanus besnardi Bernasconi, 1955a:92; 1955b:56, figs. 1–9, pl. 1: figs. 2, 6; pl. 7: fig. 2a–c.—Brito, 1962:5, pl. 3: fig. 2; 1968: 20, pl. 9: figs. 2, 3.—Tommasi, 1967:10, figs. 1, 2.

Centrostephanus longispinus rubricingulus.—Serafy, 1979:28, fig. 8.

SPECIES NAME.—In his original description of this species, H.L. Clark (1921:108) spelled the species name as *rubicingulus*. In a footnote, Clark stated that the name was derived from "rubus = red + cingulus = a zone or band, in references to the banded spines." Here Clark was in error, for *rubus* translates from Latin as a bramble or blackberry. In a later paper (Clark, 1925) he spelled

TABLE 1.—Measurements of *Centrostephanus longispinus longispinus* from the eastern Atlantic (Atl. = *Atlantide* Expedition stations; MCZ = Museum of Comparative Zoology, Harvard University; H.D. = horizontal diameter of test (in mm); Dia. = diameter; % H.D. = peristome or apical system diameter expressed as percentage of test diameter; Plates A and IA = number of plates in ambulacral and interambulacral columns, respectively; Wedges A and IA = number of wedges in ambital ambulacral and interambulacral spines, respectively)

Specimen	H.D.	Peristome		Apical system		Plates		Wedges	
		Dia.	% H.D.	Dia.	% H.D.	A	IA	A	IA
Atl. 106	16	7	44	6	38	11	9	14	15
Atl. 116	17	7	41	6	35	12	10	15	17
Atl. 116	20	9	45	8	40	12	10	15	17
Atl. 116	21	10	48	9	43	12	11	15	18
MCZ 689	24	10	42	9	38	14	11	17	20
Atl. 61	31	14	45	10	32	15	12	19	19
Atl. 61	40	15	38	16	40	16	13	18	21
MCZ 4573	40	16	40	17	43	16	12	18	21
Atl. 61	45	16	36	17	38	17	14	–	–

the species-name as *rubricingulus* without comment, and every subsequent author has spelled the name as *rubricingulus*. Clark's original spelling of the species name does not represent an incorrect original spelling in the sense of Article 32(c) of the *International Code of Zoological Nomenclature* (1961 edition). Clark made an incorrect transliteration and, according to the provisions of Article 32(a)(ii), this does not qualify as an inadvertent error; the original spelling must therefore be retained.

MATERIAL EXAMINED.—The description given below is based upon study of numerous live and preserved specimens collected from the east coast of Florida (see Table 2). Representative specimens have been deposited at the National Museum of Natural History, Smithsonian Institution (USNM E28068, E28069), and the Indian River Coastal Zone Museum, Harbor Branch Foundation, Inc. (IRCZM 72:330, 72:331, 72:332, 72:333, 72:334).

DIAGNOSIS.—Smaller specimens with banded spines, bands reddish brown on a whitish ground color. Larger specimens, horizontal diameter > 25 mm, with uniformly blackish spines or banded spines, the bands brown on a lighter brown ground color. Western Atlantic.

TYPE-LOCALITY.—Off Barbados, British West Indies.

DESCRIPTION.—Characters of test and spines are similar to those described by Mortensen (1940) for *C. rubicingulus*, although supposed differences between *C. longispinus* and *C. rubicingulus* noted by Mortensen are apparently not significant, as pointed out by Fell (1975) and by the present authors (see "Remarks," p. 11). Information on the numbers of test plates, the diameter of peristome and apical system, and on the structure of spines, is presented in Table 3.

In natural light, overall color of living specimens appears uniformly black, except for distinctively colored claviform spines and lighter colored bases of primary spines. Under artificial light, the apical system is reddish brown, madreporic plate darker. Anal funnel and spines on the periproct are dark brown. On the plates surrounding the apical system, the proximal portion is deep reddish brown; the distal portion and all other plates are lighter reddish brown. Thus a dark ring is formed around the apical system. Claviform spines are reddish brown proximally, tipped with intense pink or purple pigment. Primary and secondary spines are dark reddish brown to black; the bases of the primary spines are light reddish

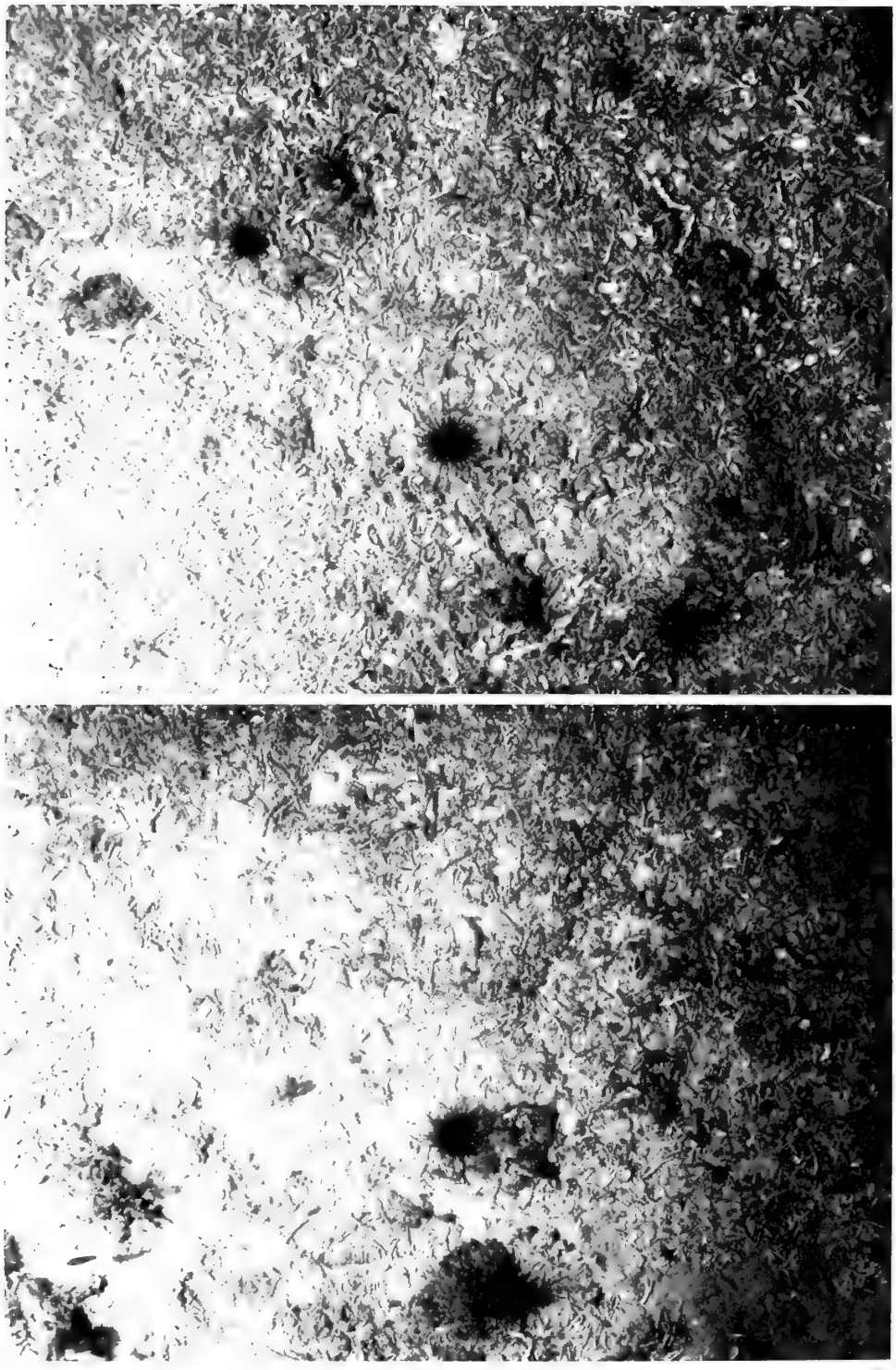


FIGURE 3.—Upper and lower, *Centrostephanus longispinus rubicingulus* H.L. Clark, photographed from *Johnson-Sea-Link* submersible on sea floor off Sebastian, Florida, 27°49.7′N, 79°58.2′W, at 58 m (note dense aggregations of dead *Oculina* coral rubble in area).

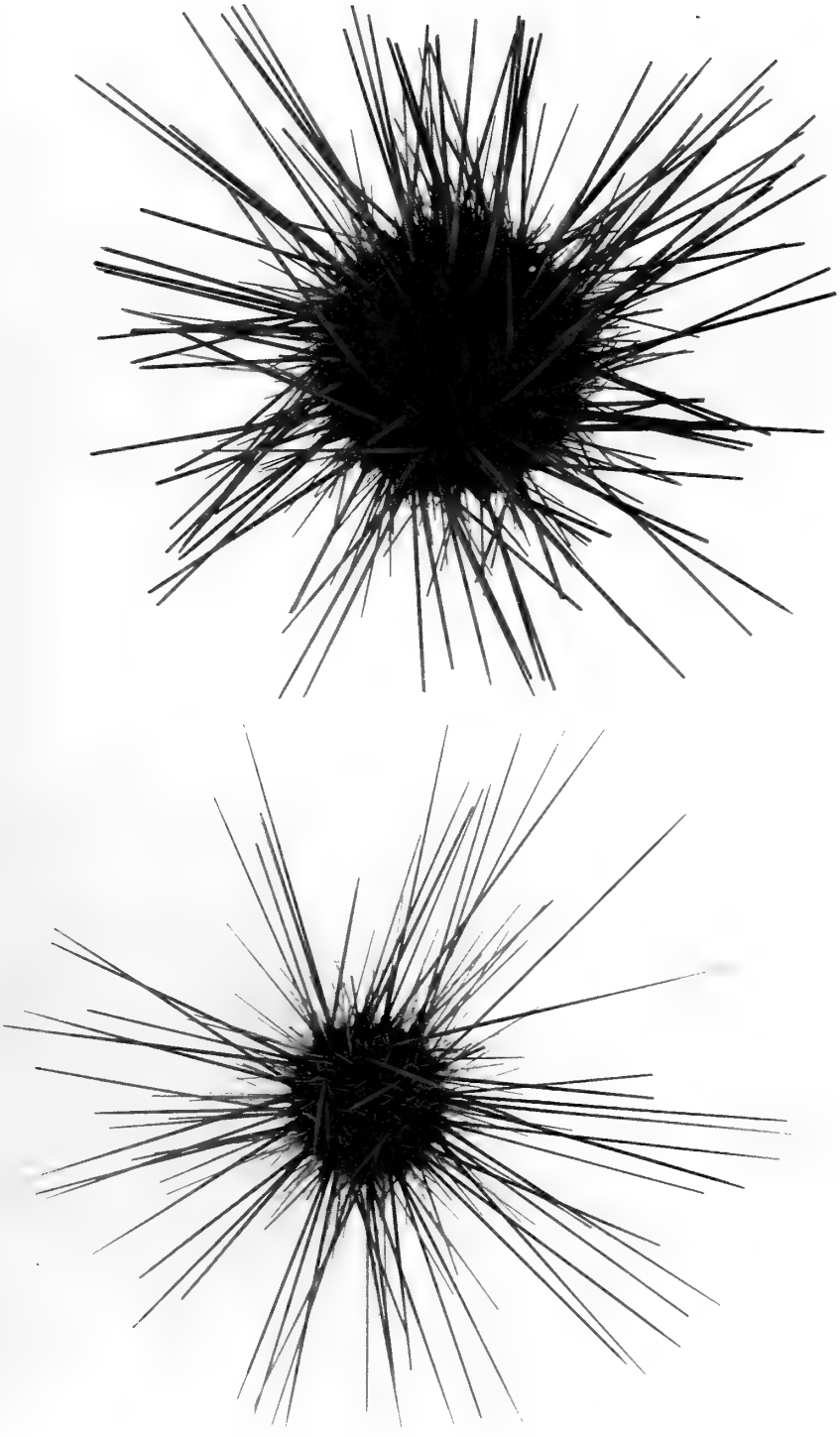


FIGURE 4.—*Centrostephanus longispinus rubicingulus* H.L. Clark, from off Sebastian, Florida: upper, specimen of 48 mm horizontal diameter; lower, specimen of 34 mm horizontal diameter.

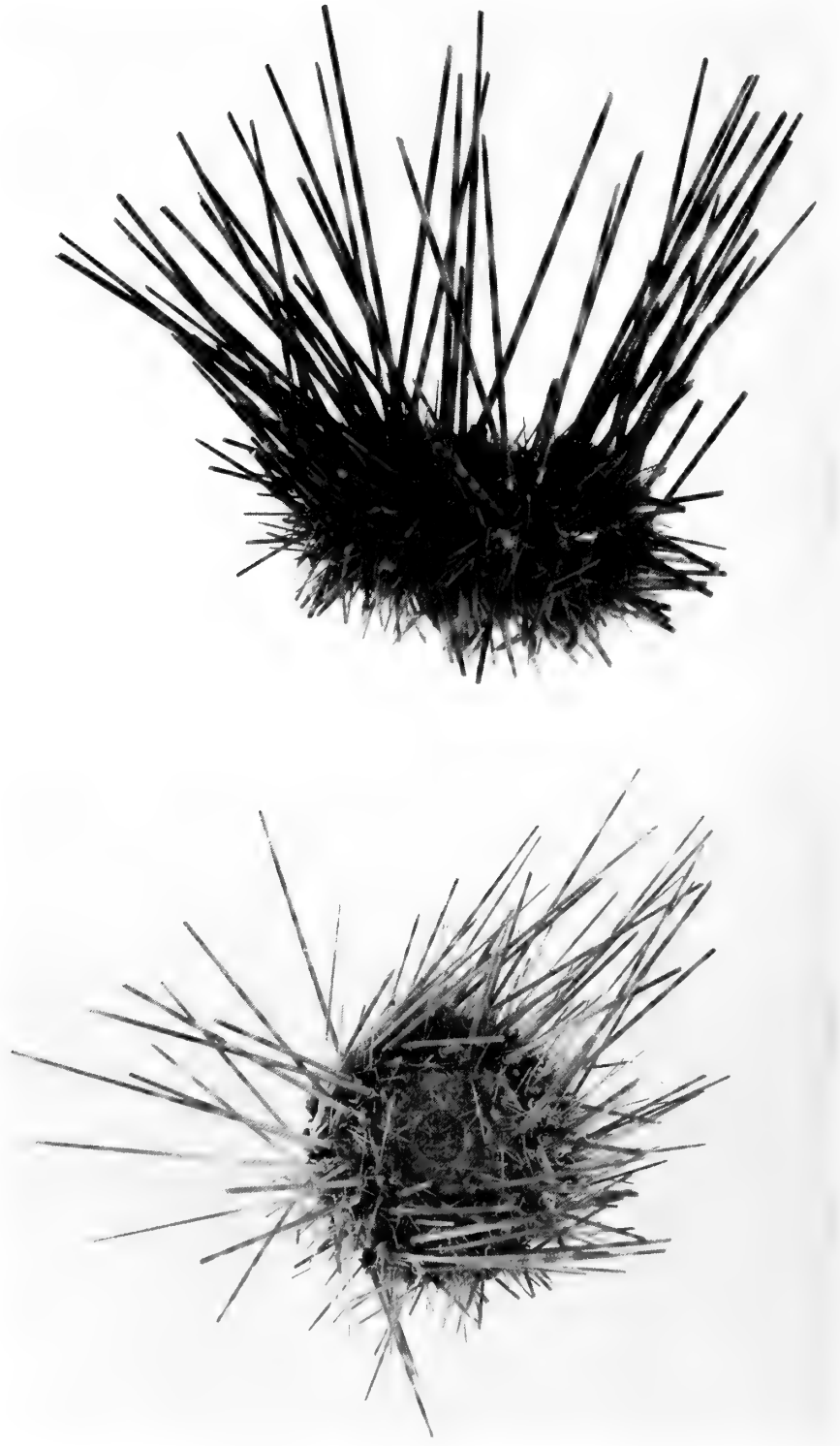


FIGURE 5.—Upper: *Centrostephanus coronatus* (Verrill), from Gulf of California, horizontal diameter 33 mm; lower: *Centrostephanus longispinus rubicingulus* H.L. Clark, light-colored form from Gulf of Mexico, horizontal diameter 37 mm (note banding of spines).

TABLE 2.—Geographic and bathymetric distribution of *Centrostephanus longispinus rubicingulus* off east central Florida, compiled from observations and collections by *Johnson-Sea-Link* submersibles

Locality	Coordinates	Depth (m)
Daytona Beach	28°57.7′N, 80°06.5′W	66–84
Cape Canaveral	28°30.0′N, 80°10.4′W	43
	28°29.6′N, 80°01.2′W	70
	28°29.6′N, 80°06.5′W	51
	28°29.5′N, 80°01.7′W	48
Satellite Beach	28°08.6′N, 79°59.6′W	73
Sebastian	27°50′11.7″N, 79°57′59.8″W	79
	27°50′02.4″N, 79°58′08.3″W	67
	27°49.7′N, 79°58.2′W	53–58
	27°46′07.7″N, 79°58′10.5″W	85
	27°46.0′N, 79°58.6′W	54
	27°43.8′N, 79°58.4′W	60–70
	27°43.8′N, 79°58.0′W	73
St. Lucie Inlet	27°12.5′N, 80°08.2′W	40

brown, uniformly flecked with brown pigment spots. The podia are dark brown when contracted, flecked with reddish brown pigment spots when expanded. The peristome is creamy white, except for triangular areas adjacent to ambs, which are flecked with light brown spots. The spines around the peristome are white, with light orange tips. The cleaned test is green to yellowish white.

In the USNM collections are several lots of small (<20 mm h.d.) specimens of this subspecies; all have reddish brown bands on white ground color on their primary spines. Two additional specimens, one of 32 mm h.d. from Sebastian, Florida, and one of 37 mm h.d. from the Gulf of Mexico, also have distinctly light-colored, banded spines, although in these cases the bands are darker brown on a lighter brown ground color. It is possible that the black-spined adults are derived from younger specimens with banded spines, as in *Diadema* species (Mortensen, 1940). Alternatively it is possible that populations of specimens with banded spines occur elsewhere in the Florida-Caribbean area, and they have yet to be adequately sampled.

Concerning the black color of the spines in the east Florida specimens, one of us (J.E.M.) has noted that when these spines are immersed in liquid bleach, the black pigment disperses, and it becomes evident that the spines are banded with light and dark brown bands. In the field, occasional specimens have a very light-colored aboral surface and spines. In light of recently published information, (Weber and Dambach, 1972), on ameboid movement of pigment cells in *C. longispinus longispinus*, a study of the pigmentation of this western Atlantic form would undoubtedly be rewarding.

DISTRIBUTION.—Western Atlantic, from Florida to Brazil and Gulf of Mexico, 33–310 meters. Black, long-spined echinoids, usually referred to as "*Diadema*" (those collected or photographed in depths greater than 40 meters along the U.S. east coast from North Carolina to Florida), probably also represent this subspecies.

HABITAT.—Serafy (1979) found *Centrostephanus longispinus rubicingulus* on algal substrata (*Lithothamnion* spp.) in the Gulf of Mexico off Egmont Key and Sanibel Island, 55–73 m. During this study we examined specimens collected from shelf-edge prominences off east central Florida, from Daytona Beach to St. Lucie Inlet, 40–85 m (see Table 2). Many of these outcroppings are covered with a dense layer of rubble, remains of the reef-building scleractinian coral, *Oculina varicosa* Lesueur. In addition to *Centrostephanus*, these

TABLE 3.—Measurements of *Centrostephanus longispinus rubicingulus* from western Atlantic (first 11 specimens with uniformly blackish spines, last 4 with banded spines; abbreviations as in Table 1; also Whorls A and IA = number of whorls per 1 cm of spine length in ambulacral and interambulacral spines, respectively)

Locality	H.D.	Peristome		Apical system		Plates		Wedges		Whorls	
		Dia.	% H.D.	Dia.	% H.D.	A	IA	A	IA	A	IA
Sebastian	24	13	54	8	33	13	11	14	15	18	17
Sebastian	25	13	52	8	32	13	11	14	15	19	18
Sebastian	27	14	52	9	33	13	11	17	19	20	19
Sebastian	32	14	44	10	31	14	12	–	–	18	17
Sebastian	37	19	51	14	36	15	12	19	22	18	18
Sebastian	44	22	50	18	40	15	12	18	18	20	20
Sebastian	45	23	51	18	40	16	13	20	21	–	–
Daytona Beach	47	23	49	17	36	18	14	20	21	16	14
Sebastian	48	24	50	18	36	18	15	20	21	19	17
Sebastian	48	22	46	17	35	18	15	19	23	19	17
Sebastian	50	24	48	18	35	17	13	20	23	18	18
Puerto Rico	18	8	44	6	33	10	9	13	6	–	–
Puerto Rico	22	11	51	9	42	12	11	12	11	–	–
Sebastian	32	–	–	–	–	–	–	16	16	–	–
Gulf of Mexico	37	–	–	–	–	–	–	18	18	–	–

rubble zones support a rich and diverse invertebrate fauna of mollusks, echinoderms, polychaetes, decapods, and encrusting organisms (see Avent et al., 1977; Reed, 1980; Reed et al., 1982). Reed (1980) mapped numerous *Oculina* reefs, both living and dead, that occur off east central Florida in depths of 50–100 m. Our in situ observations of *C. longispinus rubicingulus* with the submersibles confirm that this subspecies is restricted to dead reefs.

Several possibilities could explain the absence of *Centrostephanus* from living reefs. Living *Oculina* reefs support large schools of fish that seek shelter within the confines of the reef matrix. Predation pressure by these fish, as well as the suspension-feeding coral polyps, may exclude juvenile and larval *Centrostephanus* respectively. Alternatively, the lack of suitable substratum for the settlement and metamorphosis of urchin larvae (i.e., living coral branches) might limit recruitment. In addition the living coral community provides less available space for the attachment of leafy algae and encrusting organisms, thereby limiting potential food resources for the urchins; leafy algae have not been reported from living *Oculina* reefs (J. Reed, pers. comm.).

As noted by Avent et al. (1977), *C. longispinus rubicingulus* usually occurs on the summits and sides of dead *Oculina* reefs. Though the bases of these reefs commonly extend to a depth of 100 m, *Centrostephanus* restricts its depth to 75–80 m, in apparent response to a distinct pycnocline and thermocline occurring at that depth.

POPULATION DENSITIES.—Throughout the year, *C. longispinus rubicingulus* were found in densities up to 5 individuals per m^2. Commonly co-existing with *Centrostephanus* are large populations of the cidaroid urchin, *Stylocidaris affinis* (Philippi), which achieves densities up to 80–100 individuals per m^2.

BEHAVIOR.—Laboratory-maintained specimens are photo-negative. A sudden increase or decrease of illumination evokes a rapid response of the primary spines that normally wave or rotate incessantly. The small claviform spines are especially sensitive to varying light intensities.

Under intense artificial light from a fiber optics illuminator, the claviform spines initially wave vigorously and cease all movement after approximately 10 minutes. Reduction of light intensity induces resumption of normal movement.

Any slight mechanical stimulation also elicits a rapid reflex action, presumably defensive in nature. Similar reactions have been noted by von Uexkull (1896) in *C. longispinus longispinus*.

Feeding.—In contrast to its congener, *C. coronatus*, which hides in crevices during the daylight and emerges only at night to feed (Nelson and Vance, 1979), *C. longispinus rubicingulus* actively forages in daylight. The coral rubble habitat of adult *C. longispinus rubicingulus* provides little refuge from predators, although juveniles perhaps receive some protection in the rubble.

During the months of June through September, various species of leafy algae have been observed attached to the coral rubble substratum. An examination of intestine contents of resident *Centrostephanus* revealed the remains of several of these species of red algae:

Rhodophyta
- Delesseriaceae
  - *Searlesia subtropica* (Schneider) Schneider and Eiseman
  - *Apoglossum ruscifolium* (Turner) J. Agardh
  - *Hypoglossum tenuifolium* (Harvey) J. Agardh
  - *Nitophyllum* species
- Kallymeniaceae
  - *Kallymenia limminghii* Montagne
- Rhodymeniaceae
  - *Leptofauchea rhodymenioides* Taylor

Diet during those months in which leafy algae is absent is unknown. However, the presence year-round of large, successful populations of urchins suggests that *C. longispinus rubicingulus* can also exist on a varied diet of small invertebrates, encrusting organisms, and drift algae. Vance (1979) reported a similar diet for *C. coronatus* off Catalina Island, California.

In the laboratory, we have maintained several specimens in closed-system aquaria for up to two years. These specimens fed on fresh shoots of the seagrass *Thalassia testudinum*. Starved specimens have been observed to prey upon the arms of the sea star *Narcissia trigonaria* Sladen.

Sexual Dimorphism.—In specimens of Florida *C. longispinus rubicingulus*, males possess conspicuous tubular genital papillae while females have short conical papillae. Through a brief survey of museum specimens, we were able to determine that the following species of *Centrostephanus* also display this type of sexual dimorphism: *C. longispinus longispinus* (Philippi), *C. rodgersii* (A. Agassiz), and *C. coronatus* (Verrill). It is probable that all species in the genus are sexually dimorphic. This type of sexual dimorphism is probably more common among echinoids than formerly supposed (Chia, 1977; Pawson and Miller, 1979).

Remarks.—In commenting on *C. rubicingulus*, Mortensen (1940:310) noted the "general resemblance to *longispinus* in nearly all characters." He listed several supposed differences in the interambulacral tubercle size and distribution, in the number of wedges in primary spines, and in the tridentate and ophicephalous pedicellariae. As examination of our newly acquired material of *C. longispinus rubicingulus* demonstrates, the only consistent difference, at least in adult specimens, lies in the one character that Mortensen (1940) dismissed, namely the coloration of spines.

Bernasconi (1955a,b) based her species *C. besnardi* on two small specimens, h.d. 12 and 18 mm, from Isla Trindade, off Brazil. In her detailed description, Bernasconi noted that *C. besnardi* differs from *C. longispinus* in various characters of the apical system, the rostrate pedicellariae, and the spine coloration. In the apical system of *C. besnardi*, ocular plates are all exsert, and the plates are essentially naked, except for the presence of a single secondary tubercle. According to Mortensen (1940:303), the position of the ocular plates, either insert or exsert, as well as the tuberculation of the apical system plates, can vary considerably in *C. longispinus*. The rostrate pedicellariae of *C. longispinus* are also variable in shape (Mortensen, 1940:305). Bernasconi's description (1955b:59) and figures of rostrate pedicellariae do not provide a clear indication that the rostrate pedicellariae of *C. besnardi* are distinctive. Coloration of the spines in *C. besnardi* (white and claret colored bands) seem to differ in no important aspect from that in juvenile *C. longispinus rubicingulus*. Al-

TABLE 4.—Measurements of *Centrostephanus coronatus*, from lower California (see Tables 1 and 3 for abbreviations; also, AHF = Allan Hancock Foundation)

Specimen	H.D.	Peristome		Apical system		Plates		Wedges		Whorls	
		Dia.	% H.D.	Dia.	% H.D.	A	IA	A	IA	A	IA
AHF 8.38	28	14	50	–	–	14	11	20	21	18	18
AHF 8.43	41	20	49	10	24	14	12	21	23	15	17
AHF 6.30	46	22	48	11	24	–	–	23	24	16	16
AHF 6.30	48	22	46	11	23	17	13	22	25	16	15
AHF 8.34	49	27	55	13	27	18	13	22	27	18	16
AHF 8.43	55	25	45	14	25	17	14	27	28	16	17
AHF 8.43	56	25	45	13	23	19	14	25	21	20	19
AHF 8.36	60	25	42	–	–	–	–	26	22	16	16

though type specimens of this species are not available for study, it seems evident that *C. besnardi* falls within the range of variation of *C. longispinus rubicingulus*, and the species are herein regarded as synonymous. Fell (1975) has already suggested that *C. besnardi* might be at best a subspecies of *C. longispinus*.

Centrostephanus coronatus (Verrill)

FIGURES 1, 2, 5; TABLES 4, 5

Echinodiadema coronata Verrill, 1867:295.

Centrostephanus coronatus.—Mortensen, 1940:314, pls. 36: figs. 7–10, pl. 76: figs. 1–4 [complete synonymy up to 1938].—H.L. Clark, 1948:237, 244, pl. 39: fig. 10.—Fell, 1975:181.—Morris, Abbott, and Haderlie, 1980:162, pl. 51: fig. 11.2a,b.

MATERIAL EXAMINED.—Allan Hancock Foundation, University of Southern California: Lower California (6.30, 8.34, 8.36, 8.38, 8.43), eight specimens; Gulf of California (8.27, 8.28), six specimens. National Museum of Natural History, Smithsonian Institution: Gulf of California (USNM 17441, USNM 32472), five specimens.

DIAGNOSIS.—Like *Centrostephanus longispinus*, except that diameter of apical system usually 24%–34% of test diameter. Spines may virtually lack trabeculae between wedges.

TYPE-LOCALITY.—Cabo San Lucas, Gulf of California.

DISTRIBUTION.—Mortensen (1940) noted that *C. coronatus* was known only from the Gulf of California to 3 fathoms. The species also occurs at the Galapagos Islands and in lower California (including offshore islands) where it is common in depths of 3–10 meters (H.L. Clark, 1948; see Pearse, 1972).

REMARKS.—H.L. Clark (1921:109) noted that "in every way" his *C. rubicingulus* is nearest to *C. coronatus*. Mortensen (1940:310) disagreed, and later (p. 315, et seq.) alluded to differences in characters of test, spines, pedicellariae, and color that could distinguish *C. coronatus* from *C. longispinus*. Our investigations of additional material revealed the following information.

In examining the interambulacra, Mortensen (1940:317) noted that in *C. coronatus* only the uppermost interambulacral plates carry claviform spines, whereas in *C. longispinus* ". . . the two uppermost plates often carry a claviform spine, and are without a primary tubercule . . . ." In our material of *C. longispinus*, more often than not, there is only a single adapical interamb plate with a claviform spine. Furthermore, in *C. coronatus*, several instances occur in which the two uppermost interamb plates carry claviform spines. Thus, this character is not reliable.

Regarding the apical system, Mortensen (1940) stated that in *C. coronatus* the apical system is 25%–27% of the horizontal diameter, while in *C. longispinus* it is 35%–40%. Our material shows that in *C. coronatus* the apical system is 24%–34% h.d., while in *C. longispinus* it is 31%–40% h.d. (see Tables 1, 3, 4, and 5; Figure 1). There is a slight

TABLE 5.—Measurements of *Centrostephanus coronatus*, from Gulf of California (see Tables 1 and 3 for abbreviations; also, USNM = United States National Museum, collections in National Museum of Natural History, Smithsonian Institution; Mrtsn. = Mortensen collection; AHF = Allan Hancock Foundation)

Specimen	H.D.	Peristome		Apical system		Plates		Wedges		Whorls	
		Dia.	% H.D.	Dia.	% H.D.	A	IA	A	IA	A	IA
USNM 32472	13	6	46	4	31	11	9	16	18	–	–
USNM 17441	26	12	46	8	29	15	12	18	20	27	26
Mrtsn. 1940	28	13	46	7.5	27	14–15	11–12	–	–	28	25
AHF 8.27	30	16	53	–	–	16	12	20	21	26	30
USNM 17441	32	16	50	11	34	17	12	17	19	25	22
USNM 17441	34	17	50	11	32	17	12	18	20	24	22
AHF 8.27	34	17	50	8	24	15	12	23	26	23	25
AHF 8.27	35	16	46	10	29	16	12	22	27	25	22
AHF 8.27	40	19	48	11	28	15	13	–	–	–	–
AHF 8.27	41	17	41	10	24	16	13	24	25	22	21
AHF 8.28	43	19	44	10	23	18	13	23	25	23	24
USNM 17441	50	–	–	–	–	–	–	22	24	–	–
Mrtsn. 1940	55	27	49	15	27	18–19	15–16	–	–	–	–
Mrtsn. 1940	62	–	–	–	–	–	–	–	–	–	–

overlap in these proportions, but apical system sizes do appear to differ consistently in the two "species."

Supposed differences in spine coloration, noted by Mortensen (1940), are eliminated by our new Florida material. In large specimens of *C. coronatus*, the spines are nearly black and the same is true for *C. longispinus rubicingulus*, at least in East Florida populations. One usually consistent difference between the two species lies in the trabecules between the spokes of the spines; in *C. longispinus* trabecules are conspicuous, while in *C. coronatus* they are virtually non-existent (Mortensen, 1940).

The number of verticillations (whorls of spinelets) on the spines provide some evidence that there may be two distinct subspecies of *C. coronatus* (see Tables 4 and 5; Figure 2). In Gulf of California specimens, the number of verticillations in ambulacral and interambulacral spines usually exceeds 20 per cm of spine length; in California specimens examined, there are usually fewer than 20 verticillations per cm of spine length. A more detailed survey of California specimens from several habitats is required before the status of the California and Gulf of California populations is settled. In *C. longispinus rubicingulus* spines usually have fewer than 20 whorls of spinelets per cm of spine length, and thus in this character the western Atlantic *Centrostephanus* most closely resembles the California coast populations of *C. coronatus*.

The relatively trivial differences between *C. coronatus* and *C. longispinus* might seem to justify uniting them under a single species name. We hesitate to take this step because it would appear to serve no useful purpose. It is important to note, however, that these species are indeed closely related, contrary to Mortensen's (1940) contentions.

Literature Cited

Agassiz, A.

1863. Synopsis of the Echinoids Collected by Dr. W. Stimpson in the Pacific Exploring Expedition under Captains Ringgold and Rodgers. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1863:352–361.

Agassiz, A., and H.L. Clark

1907. Preliminary Report on the Echini Collected in 1902, among the Hawaiian Islands by the U.S. Fish Commission Steamer *Albatross*, in Charge of Commander Chauncey Thomas, U.S.N., Commanding. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 50(3):229–272.

Alvarado, R., and J. Alvarez

1964. Resultados de la expedicion Peris-Alvarez a la isla de Annobon, VIII: Algunos invertebrados marinos. *Boletin de la Real Sociedad Española de Historia Natural, Biologica*, 62:265–282, 5 figures.

Avent, R.M., M.E. King, and R.H. Gore

1977. Topographic and Faunal Studies of Shelf-Edge Prominences off the Central Eastern Florida Coast. *Internationale Revue der Gesamten Hydrobiologie*, 62(2):185–208.

Bernasconi, I.

1955a. Una nueva especie de Diadematidae tropical. *Neotropica*, 1:92.

1955b. Equinoideos y asteroideos de la colleccion del Instituto Oceanografico de la Universidad de San Pablo. *Boletin del Instituto Oceanografico*, 6:51–77, plates 1–7.

Brito, I.M.

1962.—Ensaio de catálago dos equinodermas do Brasil. *Avulso Centro de Estudos Zoologicos, Universidade do Brasil*, 13:1–11, 3 plates.

1968. Asteróides e equinóides do Estado da Guanabara e adjacências. *Boletim do Museu Nacional do Rio de Janeiro*, new series (Zoologia), 260:1–51, 15 plates.

Chapman, G.

1955. Aspects of the Fauna and Flora of the Azores, IV: Echinodermata. *Annals and Magazine of Natural History*, 12(8):398–400.

Cherbonnier, G.

1956. Les échinodermes de Tunisie. *Bulletin Station Océanographique Salammbo*, 53:1–23, 1 figure.

1959. Echinides. *Résultats Scientifiques Expédition Océanographique Belge dans les Eaux Côutières Africaines de l'Atlantique Sud (1948–1949)*, 3(6):35–59, 10 plates, 1 figure.

1963. Echinodermes des côtes du Cameroun récoltés par A. Crosnier en Décembre 1962-Janvier 1963. *Bulletin du Muséum d'Histoire Naturelle, Paris*, 35:179–193, 3 figures.

Chesher, R.H.

1966. The R/V *Pillsbury* Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65, 10: Report on the Echinoidea Collected by R/V *Pillsbury* in the Gulf of Guinea. *Studies in Tropical Oceanography, Institute of Marine Sciences (University of Miami)*, 4(1):209–223.

Chia, F.-S.

1977. Structure and Function of the Genital Papillae in a Tropical Sand Dollar, *Arachnoides placenta* (L.), with a Discussion on the Adaptive Significance of Genital Papillae in Echinoids. *Journal of Experimental Marine Biology and Ecology*, 17:187–194.

Clark, A.H.

1954. Echinoderms (Other than Holothurians) of the Gulf of Mexico. *Bulletin of the United States Fish Commission*, 55:373–379.

Clark, H.L.

1914. Echinoderms of the Western Australian Museum. *Records of the Western Australian Museum*, 1:132–173, plates 17–26.

1921. Report on the Echinoidea Collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *University of Iowa Studies in Natural History*, 9(5):103–121, 2 plates.

1925. *A Catalogue of the Recent Sea-Urchins (Echinoidea) in the Collection of the British Museum (Natural History).* i–xxxiii + 250 pages, 12 plates. London: British Museum (Natural History).

1948. A Report on the Echini of the Warmer Eastern Pacific, Based on the Collections of the *Velero III. Allan Hancock Pacific Expeditions*, 8(5):225–351, figures 1–3, plates 35–71.

Fell, F.J.

1975. The Echinoid Genus *Centrostephanus* in the South Pacific Ocean with a Description of a New Species. *Journal of the Royal Society of New Zealand*, 5(2):179–193, figures 1–6.

Hamann, O.

1887. Beitrage der Histologie der Echinodermen. *Jenaische Zeitschrift für Naturwissenschaft*, 21:87–266, plates 6–18.

International Commission for Zoological Nomenclature

1961. Article 32(c): Incorrect Original Spelling. *International Code of Zoological Nomenclature*, 15(1):35.

Koehler, R.
1895. Notes Echinologiques. *Revue Biologique du Nord de la France*, 7:317–342, plate 9.

Lewis, J.B.
1961. List of the Echinoidea of Barbados. *Journal of the Barbados Museum of Natural History Society*, 28(2):52–53.

Märkel, K.
1970. Morphologie der Seeigelzahne, 3: Die Zahne der Diadematoida und Echinothuroida (Echinodermata, Echinoidea). *Zeitschrift für Morphologie und Ökologie der Tiere, Berlin*, 66:189–211, 20 figures.

Millott, N.
1957. Animal Photosensitivity, with Special Reference to Eyeless Forms. *Endeavour*, 16(61):19–28, 21 figures.

Morris, R.H., D.P. Abbott, and E.C. Haderlie.
1980. *Intertidal Invertebrates of California*. ix + 690 pages, 290 plates. Stanford: Stanford University Press.

Mortensen, T.
1904. The Danish Expedition to Siam, 1899–1900, II: Echinoidea (1). *Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark*, 7th series, 1(1):1–124, 7 plates.
1940. *A Monograph of the Echinoidea, III.1: Aulodonta*. 370 pages, 197 figures, 77 plates. Copenhagen: C.A. Reitzel.
1951. Report on the Echinoidea Collected by the "Atlantide" Expedition. *Atlantide Report*, 2:293–303, 1 figure, 2 plates.

Nelson, B.V., and R.R. Vance
1979. Diel Foraging Patterns of the Sea Urchin *Centrostephanus coronatus* as a Predator Avoidance Strategy. *Marine Biology*, 51:251–258.

Pawson, D.L., and J.E. Miller
1979. Secondary Sex Characters in *Coelopleurus floridanus* A. Agassiz, 1872 (Echinodermata: Echinoidea). *Bulletin of Marine Science*, 29(4):581–586, 2 figures.

Pearse, J.S.
1972. A Monthly Reproductive Rhythm in the Diadematid Sea Urchin *Centrostephanus coronatus* (Verrill). *Journal of Experimental Marine Biology and Ecology*, 8:167–186.

Philippi, R.
1845. Beschreibung einiger neuen Echinodermen. *Archiv für Naturgeschichte*, 1845:351–354.

Reed, J.K.
1980. Distribution and Structure of Deep-Water *Oculina varicosa* Coral Reefs off Central Eastern Florida. *Bulletin of Marine Science*, 30(3):667–677.

Reed, J.K., R.H. Gore, L.E. Scotto, and K.A. Wilson
1982. Community Composition, Structure, Areal and Trophic Relationships of Decapods Associated with Shallow- and Deep-Water *Oculina varicosa* Coral Reefs. *Bulletin of Marine Science*, 32(3):761–786.

Repelin, R.
1962. Echinidae du plateau continental gabonais et congolaais en collection au centre d'oceanographie de Pointe-Noire. *Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer (Océanographie)*, 2:1–7, 5 plates.

Serafy, D.K.
1979. Echinoids (Echinodermata: Echinoidea). *Memoirs of the Hourglass Cruises*, 5(3): 120 pages, 47 figures.

Tommasi, L.R.
1967. Lista dos Equinoides recentes de Brasil. *Contribuições Avulsas do Instituto Oceanografico Universidade de Sao Paulo, Oceanografia Biológica*, 11:1–50, 9 plates, 72 figures.

Tortonese, E.
1953. Gli Echinodermi del Mar Ligure e della zona vicine. *Atti dell'Accademia Ligure di Scienze e Lettere*, 8:163–242, figures 1–10, plate 1.
1965. *Echinodermata: Fauna d'Italia*. Volume 6, xv + 422 pages, 186 figures. Bologna: Edizioni Calderini.
1976. Res Ligusticae 186 L'echinoide *Centrostephanus longispinus* (Pet.) en méditérrannee nord-occidentale. *Annali del Museo Civico di Storia Naturale (di Genova) Giacomo Doria*, 80:238–240.

Uexküll, J. von
1896. Der Schatten als Reiz für *Centrostephanus longispinus*. *Zeitschrift für Biologie*, 34:319–339, plates i–iii.

Vance, R.R.
1979. Effects of Grazing by the Sea Urchin, *Centrostephanus coronatus*, on Prey Community Composition. *Ecology*, 60(3):537–546.

Verrill, A.E.
1867. Notes on Radiata in the Museum of Yale College, with Description of New Genera and Species, Number 2: Notes on the Echinoderms of Panama and the West Coast of America, with Descriptions of New Genera and Species. *Transactions of the Connecticut Academy of Arts and Sciences*, 1:251–322.

Weber, W., and M. Dambach.
1972. Amöboid bewegliche Pigmentzellen im epithel des seeigels *Centrostephanus longispinus*. *Zeitschrift für Zellforschung un Mikroskopische Anatomie*, 133(1):87–102, 10 figures.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information; **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume(number):pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.